

Modeling Disjunct Gray Wolf Populations in Semi-Wild Landscapes

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Abstract: *Gray wolves (Canis lupus) in parts of the United States and Europe live in networks of disjunct populations, many of which are close to human settlement. Because wolf management goals include sustaining disjunct populations, it is important to ask what types of areas and protections are needed for population survival. To predict the effects of different levels of human-caused mortality, we created a simulation model for a disjunct wolf population living in a semi-wild landscape with abundant, well distributed prey. The landscape included a maximum of 16 territories divided into core and peripheral range. The mortality rate in the core range was 20%, whereas the mortality rate in peripheral range (40%) was higher because of human-caused deaths. We examined the relationship between the proportions of core and peripheral range and the 50-year occupancy of that range by wolf packs, given different assumptions about pup and dispersal mortality and immigration. Simulations showed that occupancy increased as the number of core sites increased, but curve location depended on parameter assumptions. With pup and dispersal mortality rates consistent with those for disease-free and legally protected populations, wolves saturated a 16-territory cluster with as few as two core sites, regardless of immigration rate. When populations had high pup or dispersal mortality, as few as two immigrants per year helped maintain high (>80%) site occupancy in clusters with four or more core sites. Small numbers of immigrants were also important for sustaining colonizing populations and buffering the negative effects of increased environmental variation. The simulations supported the claim that wolves can survive in disjunct populations provided that wolves can move between populations, human persecution is not excessive, and prey is abundant.*

Modelado de Poblaciones Fragmentadas de Lobo Gris en Paisajes Semi-Silvestres

Resumen: *En parte de los Estados Unidos y Europa, el lobo gris (Canis lupus) vive en redes de poblaciones fragmentadas, muchas de las cuales se encuentran cercanas a asentamientos humanos. Debido a que las metas de manejo del lobo incluyen el sostenimiento de poblaciones fragmentadas, es importante preguntarse que tipos de áreas y protecciones son necesarias para la sobrevivencia de una población. Para predecir los efectos de la mortalidad causada por humanos a diferentes niveles, creamos un modelo de simulación para una población fragmentada de lobos viviendo en un paisaje semi-silvestre, con una abundante y bien distribuida presa. El paisaje incluyó un máximo de 16 territorios divididos en rangos medulares y periféricos. La tasa de mortalidad en el rango medular fue de un 20% mientras que la tasa de mortalidad en el rango periférico fue de un 40%, siendo esta mayor debido a muertes ocasionadas por humanos. Examinamos la relación entre las proporciones del rango medular y periférico y la ocupación de estos rangos a lo largo de 50 años por grupos de lobos dadas diferentes condiciones de mortalidad de cachorros, dispersión e inmigración. Las simulaciones muestran que la ocupación incrementa en tanto el número de sitios medulares se incrementa; sin embargo, la curva de ubicación depende de los parámetros asumidos. Con tasas de mortalidad de*

cachorros y por dispersión consistentes con aquellas de poblaciones libres de enfermedades y legalmente protegidas, los lobos saturaron un conglomerado de 16 territorios con tan solo 2 sitios medulares, independientemente de la tasa de inmigración. Cuando las poblaciones tuvieron una mortalidad alta de cachorros o por dispersión, tan solo 2 inmigrantes por año ayudaron a mantener alta (>80%) la ocupación de sitios en clusters con cuatro o más sitios medulares. Un número pequeño de inmigrantes fue también importante para mantener colonizando poblaciones y amortiguando los efectos negativos de una variación ambiental elevada. Las simulaciones soportan la idea de que los lobos pueden sobrevivir en poblaciones fragmentadas, siempre y cuando los lobos puedan moverse entre poblaciones, que la persecución por humanos no sea excesiva y que las presas sean abundantes.

Introduction

Conservation strategies for mammalian carnivores include the management of disjunct populations, which are separated from neighboring populations by barriers that restrict but do not preclude the exchange of animals (Beier 1993; Mech 1995a). Managing disjunct populations is important because survival at a larger regional scale often depends on growth and dispersal characteristics of local populations (for review see Fahrig & Merriam 1994). We present a model for the dynamics of a disjunct population of gray wolves (*Canis lupus*) and make inferences about population survival under different levels of mortality and immigration. Although our model was designed using life-history patterns of wolves, it has features applicable to other territorial species. The model recognizes that the population is composed of social units in which breeding is limited to dominant adults and that the demographic success of each social unit depends on the quality of its habitat. The model also accounts for the dispersal of animals between social units and the movement of animals between populations.

As a result of human tolerance, reintroduction, and natural repopulation, gray wolves now live in parts of the United States and Europe from which they were once extirpated (Promberger & Schroeder 1993; Fritts & Carbyn 1995; Mech 1995a). Many areas recolonized by wolves are not wilderness but highly altered landscapes in proximity to human development. Further, many recolonizing populations are separated from source populations by distances and barriers that restrict the exchange of animals. Because management goals often include sustaining disjunct wolf populations, it is important to ask what types of areas and protections are needed for population survival.

Recovering wolf populations in the Lake Superior region of the United States (Fig. 1) exemplify disjunct populations in semi-wild landscapes. Although gray wolves originally lived throughout the Lake States (Minnesota, Wisconsin, and Michigan), European settlers nearly eliminated wolves by unregulated harvest of ungulates and intense exploitation. By 1960 wolves were limited to the

wilderness of northeastern Minnesota (contiguous to a large Canadian wolf population) and Isle Royale in Lake Superior (Mech 1970). As a result of more favorable public attitudes and legal protection under the U.S. Endangered Species Act of 1973, wolves from northeastern Minnesota were able to colonize most of northern Minnesota and parts of northern Wisconsin and northern Michigan. In the spring of 1997 the populations in Wisconsin and Michigan were each between 100 and 150 wolves (A. P. Wydeven, unpublished data; J. H. Hammill, unpublished data) and the Minnesota population was at least 2000 (W. Berg, unpublished data). The landscape in this range was not wilderness but a mosaic of forest, agricultural, and developed land under a variety of public and private ownerships (Mladenoff et al. 1995). Logging and agriculture created large areas of young forests that supported large populations of white-tailed deer (*Odocoileus virginianus*; Mladenoff & Stearns 1993), the preferred prey of wolves (Stenlund 1955). Colonizing wolves first settled in forested areas with few roads and little human settlement (Thiel 1985; Mech et al. 1988; Mladenoff et al. 1995). Later, wolves settled in more-developed areas with higher road and human population densities (Fuller et al. 1992). Parts of the population in central Minnesota and those in northern Wisconsin and Michigan were separated from the larger source population in northern Minnesota by Lake Superior or large areas of less favorable habitat. Further, much of the wolf mortality was human-caused, whether intentional, accidental, or indirect through disease (Fuller et al. 1992; Mech & Goyal 1993; Wydeven et al. 1995).

It is important to predict the fate of disjunct wolf populations in semi-wild areas because management objectives often include protection or control. In the Lake Superior region, for example, state agencies are developing management plans for the time when the wolf is removed from the Endangered Species List. The few long-term (>25-year) studies of disjunct wolf populations in North America suggest that populations can survive in small (e.g., 3000 km²), semi-isolated areas, provided prey is abundant and human-caused mortality is not excessive (Fritts & Carbyn 1995). We refine these results by simulating the dynamics of hypothetical disjunct wolf popu-

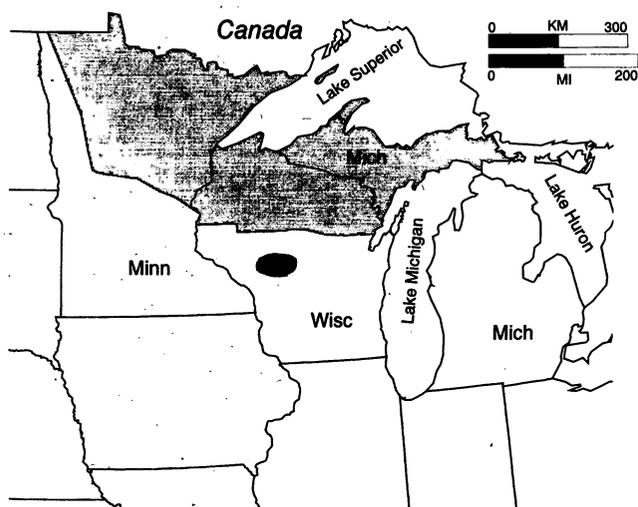


Figure 1. Shaded areas show current wolf population range in Minnesota and areas in Wisconsin and Michigan where recolonization is occurring.

lations under different assumptions about mortality and immigration.

Methods

Considerations for Model Design

A wolf pack usually consists of a breeding pair of wolves and their offspring from one or more generations (Mech 1970). In the Lake Superior region, mid-winter pack size averages four to eight wolves, about half of which are pups (Mech 1973; Mech 1987; Fuller 1989; Wydeven et al. 1995). The dominant adult female in each pack breeds yearly, usually producing a single litter of pups in spring. In North America, litter size averages four to seven pups (Mech 1970; Fuller 1989). Pups are adult-sized by winter, and most disperse when they are yearlings (Fuller 1989; Gese & Mech 1991; Wydeven et al. 1995). A dispersing wolf may pair with the opposite sex and colonize a vacant territory or may join another pack and replace a missing breeding member (Rothman & Mech 1979; Fritts & Mech 1981; Gese & Mech 1991; Meier et al. 1995). When both breeding adults die, the pack usually disintegrates, leaving the territory vacant and creating an opportunity for recolonization (Meier et al. 1995).

A wolf population can cover thousands of square kilometers with discrete but interacting packs. Wolves are not habitat-specific; they can live wherever they have sufficient prey and are tolerated by humans (Fuller et al. 1992; Mech 1995a). In the Lake Superior region, mid-winter pack territories average 150–180 km² (Fuller et al. 1992; Wydeven et al. 1995). Range expansion is facilitated by great variation in dispersal behavior: some

wolves search for territories and mate only in areas near their natal territories, whereas others move long distances (Mech 1987; Gese & Mech 1991).

Model Structure and Parameters

Our model was a variant of one developed by Haight and Mech (1997). The model was designed to simulate a disjunct wolf population living in a large, semi-wild landscape with abundant, well-distributed prey. The landscape was bounded by the assumption that it could support a maximum of 16 pack territories. If territories averaged 180 km² and 40% of the landscape was in interstitial areas (Wydeven et al. 1995), a population of 16 packs would cover about 4000 km². The territories were identified as being in either core or peripheral range. We assumed that wolves in the core range suffered less human-caused mortality than wolves in the peripheral range; otherwise, demographic processes did not vary. This assumption reflected our observation that peripheral range is distinguished by a greater likelihood of human-caused mortality and not by lower prey availability. By varying the number of territories in core range, we estimated the effects of different mortality rates on population survival.

To simulate wolf life history, we created a stage-class model for the dynamics of each pack. The model predicted the mortality, dispersal, and birth of wolves and the fate of dispersing wolves. The demographic parameters were similar to those of wolves inhabiting northcentral Minnesota (Fuller 1989) and northern Wisconsin (Wydeven et al. 1995).

Beginning on 1 October, each pack was characterized by the number of wolves of each sex in each of five stages. The stages were defined based on age and breeding status. The four age classes for nonbreeding wolves were pup (0–6 months), juvenile (6–18 months), yearling (18–30 months), and adult (≥ 30 months). The fifth stage was defined for the breeding pair, each member of which must be at least 18 months old beginning 1 October. Breeding took place in spring, so the minimum breeding age was 22 months. We assumed that pups were born in May, so the pup class contained wolves only during the spring and summer.

The annual change in number of wolves in each pack was calculated with the following sequence of events (Fig. 2). The first was winter mortality. The number of wolves that died in each life-history stage was a binomial random variable with a mean that depended on habitat quality. In the long-term simulations described below, wolves in core wolf range were subject to a 20% mean winter mortality rate, which was consistent with observations of wolves that recently colonized northern Wisconsin and suffered little human-caused mortality (Wydeven et al. 1995). Mean mortality rate in peripheral range was 40%, which was consistent with observations

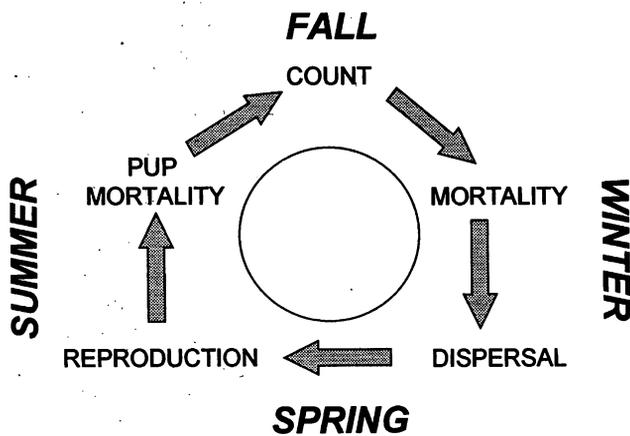


Figure 2. Sequence of events used to compute the annual change in number of wolves in each pack.

of wolf populations in northcentral Minnesota and northern Wisconsin that suffered significant human-caused mortality (Fuller 1989; Wydeven et al. 1995).

Dispersal depended on the survival of the breeding pair. If the breeding pair died, remaining pack members dispersed. If one or both breeders were present, the number of dispersers from each age class was a binomial random variable. Dispersal probabilities for juveniles, yearlings, and nonbreeding adults were 25%, 50%, and 90%, respectively, so most nonbreeding wolves dispersed before reaching 4 years old (Gese & Mech 1991).

We assumed that 20% of the dispersing wolves were long-distance dispersers that immediately emigrated from the area and thus were lost from the population. Each remaining disperser searched the area for a suitable site, which was defined as a vacant site or a site with an available mate. To account for immigration from a population outside the area, we assumed that a number of outside wolves joined this pool of dispersing wolves in the search for suitable sites. By varying the number of immigrants from zero to three wolves per year, we estimated the effects of immigration on population survival.

Each dispersing wolf (including the immigrants) was assumed to sample six suitable, replacement sites at random (see Lande [1987] and Lamberson et al. [1994] for other applications of this kind of search model). The implication of this assumption was that spatial coordinates and shapes of pack territories were not needed. The probability of finding a suitable site was 1 minus the probability of failing to find a suitable site within the given number of trials:

$$\text{Prob (success)} = 1 - \left[1 - \frac{\text{no. suitable sites}}{\text{total no. sites}} \right]^6 \quad (1)$$

A uniform random number was drawn for each dispersing wolf and compared with the probability of success. A successful wolf was randomly assigned to a site with

an available mate, and if no mate was available to a vacant site. An unsuccessful wolf was assumed to die. Thus, the survival rate of dispersing wolves depended on the maximum number of sites they were allowed to visit and the number of suitable sites. We investigated the effects of increased dispersal mortality by reducing the maximum number of site visits.

Elements of our dispersal model were consistent with observations of dispersing wolves in northern Minnesota (Gese & Mech 1991). Those authors found that 15–25% of juvenile and yearling dispersers moved more than 200 km and crossed more than 10 pack territories. Many of these dispersers seemed predisposed to moving long distances rather than searching closer to their natal territories for mates. Most of the remaining wolves traveled less than 100 km, crossing one to three territories. Many local dispersers had already engaged in predispersal forays that increased their search areas. Our assumption of a random search process is based on the observation that wolves tend to disperse in all directions equally, provided there are no physical barriers to dispersal.

A litter of pups was produced in spring if a breeding pair was present. Litter size was chosen from a discrete probability distribution with a mean of 4.5 pups and a range of zero to eight pups (Fuller 1989). The sex of each pup was a Bernoulli trial with equal probability. If only one member of the dominant pair was present, the remaining wolves held their territory but did not produce a litter. Recent evidence suggests that mother-and-son and sibling matings rarely, if ever, occur (Smith et al. 1997).

Pup mortality, which took place in summer, was modeled as a binomial random variable with probability 0.20. This rate was consistent with observations of disease-free populations in Alaska and Canada (Ballard et al. 1987; Mech 1995b). In the sensitivity analysis, we increased mean pup mortality rate to 40% to simulate the effects of canine parvovirus, a disease that recently infected wolves in Wisconsin and Minnesota and probably caused significant pup loss (Mech & Goyal 1993; Wydeven et al. 1995). Instead of defining a separate process for the summer mortality of older wolves, we assumed that any older wolves that died in summer were accounted for in the winter mortality process.

Following pup mortality, the distribution of wolves in each pack was updated by moving the surviving pups to the juvenile stage, juveniles to the yearling stage, and yearlings to the adult stage. The updated distribution approximated the situation in October and was the basis for the next year's projection.

Simulations

The first analysis was designed to check the short-term predictive ability of the wolf model. Observations of rates of population growth and mortality have been

compiled from wolf population studies throughout North America (Fuller 1989). Those observations showed a strong negative correlation between population growth and mortality. We compared those observations with model predictions of growth and mortality for a hypothetical wolf population. The initial population had 24 wolves in 4 packs living in an area with a carrying capacity of 16 packs. Population growth was computed under different mortality rates (10–50%), each applied uniformly across the cluster of sites. The exponential rate of population growth was computed using the predicted population size after 5 years, which is the average time that the real populations were observed. The pup mortality rate was 40%, and there was no immigration. Predicted population size was the mean of 1000 independent simulations.

The second analysis was used to predict the long-term effects of different assumptions about mortality and immigration on a wolf population living in an area with a carrying capacity of 16 packs. We designed four sets of simulation experiments (Table 1). Each set included 16 experiments obtained by varying the number of core sites from two to eight and the number of annual immigrants from zero to three. For each combination of number of core sites and immigration rate, the percentage of sites occupied at year 50 was computed as the mean of 1000 independent simulations. In the baseline set of experiments (A), the large initial population was close to carrying capacity with 14 packs, each including two juveniles, two yearlings, and a breeding pair. The pup mortality rate was 20%, and dispersing wolves searched a maximum of six sites. We modified this baseline set of experiments with three one-at-a-time parameter changes. In set B, experiments were conducted with higher pup mortality (40%) to predict the effects of long-term incidence of canine parvovirus disease. To predict the effects of increased dispersal mortality, experiments in set C were conducted under the assumption that dispersing wolves visited a maximum of two rather than six sites. To predict the effects of initial population size, experiments in set D used a small initial population composed of two packs in the core range.

Finally, we tested the sensitivity of the results to increased environmental variation. In population models such as ours that treat individuals in integer terms, there

are two sources of randomness in demographic processes (Simberloff 1988). Demographic stochasticity is the sampling variation among members of the population obtained by treating demographic processes such as winter mortality as binomial random variables. Environmental stochasticity is the year-to-year variation in the means of the binomial distributions. The simulation experiments described above contained demographic stochasticity but no environmental stochasticity because demographic processes were binomial random variables with means that were constant over time. We added environmental variation by randomizing the means of the demographic processes and repeated each of the four sets of simulation experiments (Table 1).

We assumed that environmental variation represented prey fluctuations. It is well known that rates of pup mortality, yearling and adult dispersal, and intraspecific mortality increase when food supply drops (Messier 1985; Ballard et al. 1987; Peterson & Page 1988; Fuller 1989; Gese & Mech 1991). Furthermore, evidence suggests that ungulate density depends more on the cumulative effect of the previous winter's snow depth than it does on wolf numbers (Mech et al. 1987; McRoberts et al. 1995). Therefore, it was reasonable to assume that ungulate availability fluctuated independently of wolf density in a nonrandom pattern involving runs of above- and below-average levels.

To capture these relationships, we modeled environmental variation using first-order autoregressive processes (e.g., Granger & Newbold 1986) for the mean rates of winter mortality, dispersal, and pup mortality. For example, letting $x(t)$ be the mean winter mortality rate in year t and μ be the long-term average winter mortality rate, the sequence of mean winter mortality rates was computed using

$$x(t + 1) = \beta x(t) + \mu(1 - \beta) + \epsilon(t) \quad \text{for } t = 1, 2, \dots, \quad (2)$$

where β was the autoregressive parameter and $\epsilon(t)$ was a normally distributed random error with mean 0 and standard deviation σ . For each of the mortality and dispersal processes, we set $\beta = 0.50$ because it produced runs of below- and above-average rates that lasted 3 years on average with a maximum of 20 years. This behavior reasonably matched our limited observations of prey fluctuations. Because a change in prey availability would affect rates of winter mortality, dispersal, and pup mortality in the same way, the correlation coefficients between random error terms in the different models were 1. The standard deviations of the error terms were 25% of the long-term mean rates.

To judge the realism of simulation model predictions, we needed estimates of realistic levels of annual variation in demographic processes to compare with variation produced in model simulations. We estimated annual variation in winter mortality, dispersal, and pup mortality from published observations of a wolf popula-

Table 1. Parameter values for the four sets of simulation experiments set up to predict effects of mortality and immigration assumptions on a wolf population.

Set	Pup mortality rate	Maximum number of site visits	Initial population
A	0.20	6	large
B	0.40	6	large
C	0.20	2	large
D	0.20	6	small

tion in northern Minnesota (Fuller 1989). For comparison we estimated annual variation in these processes from the simulations that contained only demographic stochasticity. Then we estimated the increase in annual variation from simulations that contained both demographic and environmental stochasticity.

Results

The relationship between short-term predictions of population growth and mortality of a hypothetical population of 24 wolves closely matched short-term observations of growth versus mortality of North American wolf populations (Fuller 1989; Fig. 3). The exponential rates of population growth were negatively correlated with mortality and suggested that population size would stabilize with a mortality rate of about 35%. The shape of the relationship between growth and mortality was highly sensitive to the rate of pup mortality and the number of immigrants. With 20% pup mortality, population growth became negative only for adult mortality rates greater than about 45%. The relationship was similar with four immigrants per year. Increased pup survival and immigration increased the likelihood that dispersing wolves found mates and reproduced, thereby offsetting the negative effects of mortality.

Long-term predictions of site occupancy under the baseline set of conditions—20% mean pup mortality rate, low dispersal mortality, large initial population, and no environmental variation—suggested a favorable outlook for the survival of disjunct populations (Fig. 4a). Mean occupancy at year 50 exceeded 98%, regardless of the number of core sites and the immigration rate.

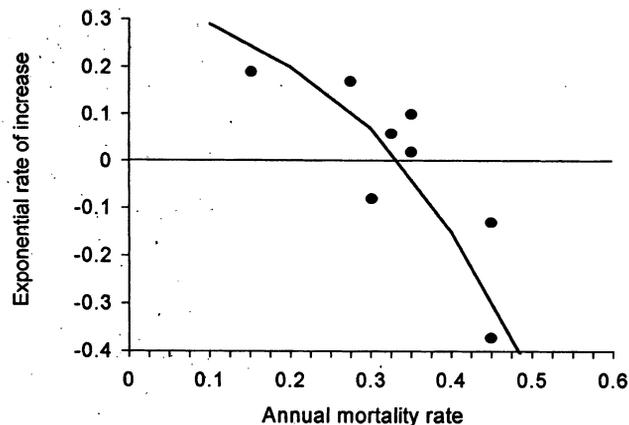


Figure 3. Predicted relationship between growth and mortality of a hypothetical wolf population in a 16-site cluster. Data points represent observations of population growth versus mortality from studies of North American wolf populations (Fuller 1989).

The population effects of immigration and the number of core sites changed when pup mortality rate was increased to 40% (Fig. 4b). With no immigration, mean site occupancy dropped when the 16-site cluster contained only 2 core sites, so by year 50 fewer than 40% of the sites contained wolves on average. Increasing either the number of core sites or the immigration rate reversed this negative trend in population size. Annual immigration of one or more wolves on four or more core sites resulted in populations that occupied at least 80% of the sites in year 50.

The effects of immigration and the number of core sites also depended on dispersal mortality. When dispersing wolves visited a maximum of two (instead of six) sites in search of mates and territory, mean occupancy in year 50 dropped, especially in areas with few core sites or immigrants (Fig. 4c). For example, with no immigration, mean occupancy in year 50 was less than 20% in areas with a two or four core sites. But as few as three immigrants per year increased site occupancy to 80% or more, regardless of the number of core sites.

The above predictions were obtained by simulating a large population that initially occupied 14 of the 16 territories. Predictions for a small population that initially oc-

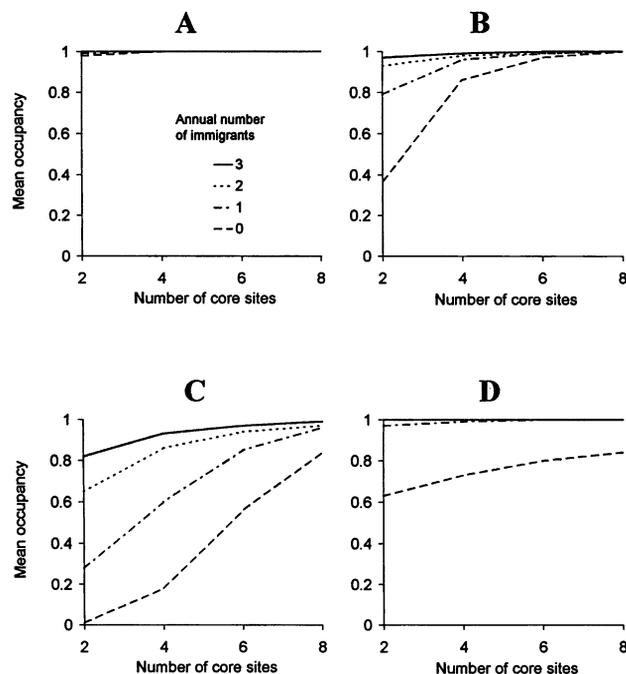


Figure 4. Mean occupancy of wolves in year 50 versus number of core sites in a 16-site cluster under different immigration rates. In the baseline set of experiments (a), the pup mortality rate was 0.20, dispersers searched a maximum of 6 sites, and the initial population was large. In (b), the pup mortality rate was 0.40. In (c), dispersing wolves visited a maximum of two sites. In (d), the initial population was small.

occupied two territories were different (Fig. 4d). Immigration played a crucial role in sustaining the growth of the small population. With no immigration, mean occupancy in year 50 was less than 80% in areas with fewer than eight core sites. With one or more immigrants per year, mean site occupancy increased to 95% or more.

The small population went extinct more often when there was no immigration. The probability that population size was less than 10 wolves in year 50 was 36% in an area with two core sites and 16% in an area with eight core sites. In contrast, the small population with one immigrant per year went extinct less than 1% of the time, regardless of the number of core sites.

To increase in size, the small population required immigration to offset mortality and increase the likelihood that dispersing wolves found mates. Without immigration, dispersing wolves had difficulty finding mates and left the cluster of sites. Emigration combined with mortality increased the likelihood of population decline. In contrast, the large population in the baseline set of simulation experiments—low pup and dispersal mortality—did not require immigration to sustain itself. With a large number of packs initially occupying the cluster of sites, dispersers from local packs were able to find mates. Consequently, immigrants were not required to repopulate vacant sites.

Annual variation in pup mortality produced by demographic stochasticity in the model was roughly consistent with an estimate of variation in a real population. We estimated the variation in annual pup mortality from published observations of a wolf population in northern Minnesota (Fuller 1989). The standard deviation of the annual pup mortality rate (0.12) was 24% of the mean rate (0.51). For comparison, the standard deviations of annual pup mortality rates (0.05–0.10) in the simulations were 15–40% of the mean rates (0.20–0.40).

To check the demographic stochasticity in the model's mortality and dispersal processes, we computed the annual variation in the percent reduction in the number of wolves between fall and spring. In the simulations the standard deviations of annual rates of loss (0.06–0.14) were 11–25% of the mean rates (0.49–0.56). From Fuller's (1989) observations, the standard deviation of annual rate of loss (0.07) was 27% of the mean rate (0.26). Thus, variation in the annual rate of loss produced by the model was less than an estimate obtained for a wild population.

Adding environmental variation by randomizing the annual rates of winter mortality, dispersal, and pup mortality by means of the autoregressive model (equation 2) increased the simulated variability in these processes beyond levels estimated from Fuller's (1989) observations. The standard deviations of simulated rates of annual pup mortality were 50–65% of the mean rates. The standard deviations of the simulated rates of annual winter loss were 30–50% of the mean rates.

Adding environmental variation resulted in lower predictions of mean site occupancy than without environmental variation (Fig. 5), but the reductions were small, especially when immigration was high. With two or three immigrants per year, for example, estimates of mean site occupancy were 0–10 percentage points less than those obtained without environmental variation. In these cases immigration buffered the effects of runs of above-average mortality and dispersal. The differences were greater in the simulation experiments with zero or one immigrant per year, especially when pup mortality was high (Fig. 5b). With little or no immigration, runs of above-average mortality resulted in more instances of population decline and increased the likelihood of population extinction.

Discussion

Our simulations imply a favorable outlook for the survival of disjunct wolf populations. Using a 16-territory cluster as a basis for prediction, we examined the relationship between the proportions of core and peripheral range and the occupancy of that range by wolf packs, given differ-

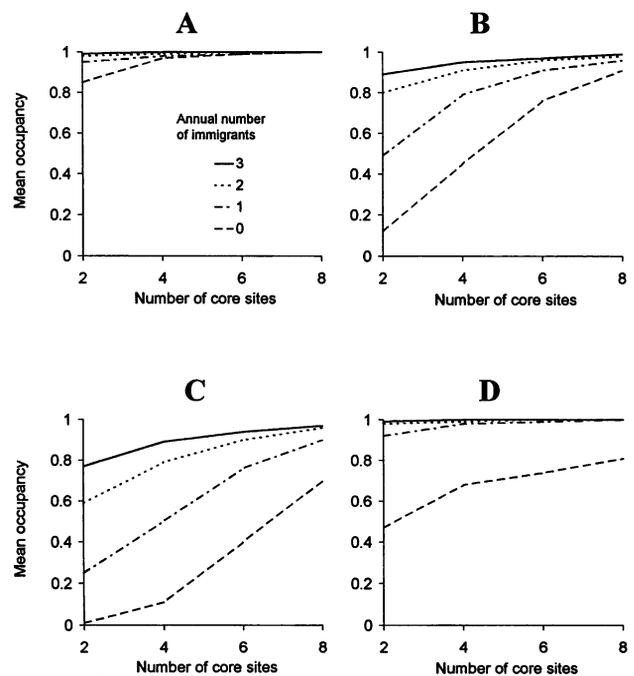


Figure 5. Mean occupancy of wolves in year 50 versus number of core sites in a 16-site cluster under different immigration rates and environmental variation. In (a), the pup mortality rate was 0.20, dispersers searched a maximum of 6 sites, and the initial population was large. In (b), the pup mortality rate was 0.40. In (c), dispersing wolves visited a maximum of two sites. In (d), the initial population was small.

ent assumptions about pup and dispersal mortality and immigration. The simulation experiments showed that the level of occupancy increased as the number of core sites and immigrants increased. With pup and dispersal mortality rates that were consistent with disease-free and legally protected populations, the wolf population saturated a 16-territory cluster with as few as two core sites, regardless of immigration rate (Fig. 4a). When populations had high pup or dispersal mortality, as few as two immigrants per year helped maintain high site occupancy (>80%) in clusters with four or more core sites (Fig. 4b, c).

The inference from our results—that a disjunct wolf population will persist in a cluster of sites that is dominated by lower-quality habitat—is strongly supported by theoretical studies. Stochastic models of metapopulation dynamics indicate that a metapopulation composed of a sufficient number of local populations each with a high rate of extinction survives because dispersal leads to recolonization of vacated sites (Fahrig & Merriam 1994; Hanski et al. 1996). Further, when birth and mortality depend on habitat quality, dispersal from local populations in high-quality habitat can maintain large populations in low-quality habitat in which reproduction does not offset mortality (Pulliam 1988). In our model each pack was a local population capable of producing many dispersers, even in low-quality habitat. These dispersers rescued packs with lost breeders or recolonized vacant sites. Of interest was our finding that reproduction and dispersal promoted population survival even when the number of peripheral sites with high mortality greatly outnumbered the number of core sites.

Our simulation results are consistent with those of empirical studies of disjunct wolf populations in Canada and the United States. Over the last 60 years a population of 40–120 wolves has lived in and around Canada's Riding Mountain National Park (3000 km²), which supports an abundant, uniformly distributed prey population (Fritts & Carbyn 1995). The park is surrounded by agricultural land, and the nearest wolf population is 45 km away. The population survived even though many of the packs were vulnerable to human exploitation. In the United States dispersing wolves from northern Minnesota began recolonizing northwestern Wisconsin in the late 1970s (Wydeven et al. 1995). The northwestern Wisconsin landscape (30,000 km²) contained wild areas each less than 3000 km² in size surrounded by lands with higher road density and human development (Mladenoff et al. 1995). In the 1980s a population of 15–40 wolves lived in wild areas despite relatively high, disease-related pup mortality and high disperser mortality from human causes. With decreasing mortality rates in the 1990s, the population grew rapidly and reached 100 wolves in 1996.

Our optimistic outlook for disjunct wolf populations is tempered by the vulnerability of small populations.

Consistent with theoretical studies of the dynamics of small populations (e.g., Ludwig 1996), our simulation experiments predicted that small, isolated wolf populations were more likely to go extinct than larger ones because fewer dispersers were present to rescue packs with missing breeders or to colonize vacant areas. But immigrants greatly reduced the vulnerability of small populations by increasing the likelihood that dispersing wolves would find mates, settle, and reproduce. An empirical study has shown that immigration sustained a colonizing wolf population subject to high mortality (Fuller 1989), and the beneficial effects of immigration have been observed in other mammalian and avian populations (Stacey & Taper 1992; Beier 1993). Consequently, it is not surprising to conclude that the growth of a colonizing wolf population is greatly enhanced by the continued immigration of a small number of wolves from outside sources.

Our model results clearly depended on the ability of dispersing wolves to find mates and vacant sites. Both the success of dispersing wolves and the consequent mean occupancy of the population decreased rapidly as the maximum number of site visits decreased. If higher dispersal mortality rates cause fewer site visits, maintaining high levels of site occupancy requires the protection of dispersing wolves as they search for mates and territories. Growing wolf populations in central Minnesota, northern Wisconsin, and northern Michigan demonstrate that, given protection against deliberate killing, dispersing wolves can successfully find mates and vacant sites in the face of accidental human-caused mortality in semi-wild landscapes. If management objectives include sustainable harvest, then careful timing and location of harvest activity combined with population monitoring might prevent excessive dispersal mortality and subsequent population decline.

It is well known that wolf abundance is positively correlated to prey density (Fuller 1989). Our model assumed that an abundant, well-distributed prey population existed over a 50-year horizon. Because we assumed no long-term negative trend in prey abundance, mean wolf mortality, dispersal, and birth rates were constant over time. A long-term reduction in prey abundance would affect a disjunct wolf population by increasing wolf mortality and dispersal rates and increasing the likelihood of population extinction.

We did model the effects of short-term prey fluctuations that result from changes in environmental factors such as cumulative winter snow depth. The relationships between the proportions of core and peripheral range and site occupancy were not very sensitive to increased environmental variation in cases where immigration was high because immigrants buffered the effects of runs of above-average mortality and dispersal. Increased environmental variation reduced site occupancy the most in situations where wolf populations

were already vulnerable: those with small numbers of core sites and few immigrants. This result suggests that long-term mean levels of wolf mortality and immigration are more important to population survival than annual short-term fluctuations in mortality and dispersal. This implies that long-term trends in environmental factors such as human-caused mortality and prey availability are more important to the survival of a disjunct wolf population than short-term fluctuations in these environmental factors.

As a result of legal protection, reintroduction, and natural repopulation, networks of disjunct wolf populations currently exist in different parts of the United States and Europe where wolves had once been extirpated. Although some of these populations live in wilderness, others live in semi-wild areas with considerable human development. Based on empirical evidence (Fritts & Carbyn 1995) and our simulation results, we believe that wolves can survive and thrive in these networks, provided that disjunct populations are linked by dispersal, human persecution is not excessive, and prey is abundant. Further, with continued protection from deliberate killing of wolves, their range will expand to semi-wild places where prey is abundant and there is some protection from accidental human-caused mortality. Examples of range expansion include Minnesota, where wolves number close to 2000 (Fuller et al. 1992), and Wisconsin and Michigan, where semi-wild areas could potentially support more than 1000 wolves (Mladenoff et al. 1997). As wolf numbers and range expand in the United States and Europe, local governments and the public will raise questions about the need for population control, especially where wolves conflict with other valued land uses (Fritts & Carbyn 1995; Mech 1995a; Mladenoff et al. 1997). Consequently, the current challenge is to develop wolf management strategies that satisfy objectives of both protection and control.

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